PROTHALLIA AND SPORELINGS OF THREE NEW ZEALAND SPECIES OF LYCOPODIUM

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 222

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(WITH PLATES II–III)

Few botanists have even seen the prothallia of *Lycopodium*, and most of those who have had such a privilege are indebted to one man, BRUCHMANN of Gotha; fewer still have made any investigation of the subject. The reason prothallia and sporelings of *Lycopodium* have not been so extensively studied as those of the ferns is not lack of interest, but difficulty in germinating the spores or finding prothallia growing naturally. In 1911 I collected adult plants of several New Zealand species of *Lycopodium* and made some effort to find prothallia, but my time was too limited for such slow, uncertain work. However, Professor A. P. W. THOMAS, at that time botanist of the University at Auckland, very kindly gave me prothallia and sporelings of 3 characteristic New Zealand species, *Lycopodium laterale*, *L. volubile*, and *L. scariosum*. Prothallia and sporelings are known in so few species that it seems worth while to give some account of this material.

Since the literature of the subject was examined with considerable care, all of the original papers cited being available, and since E. A. SPESSARD, a student of mine, is announcing in this issue of the BOTANICAL GAZETTE the first discovery of the prothallia and sporelings of several American species of *Lycopodium*, a historical résumé may be of service to those who are in favorable localities and who might wish to study the subject.

Historical

TREUB (7) introduced his classic account of the prothallium of *Lycopodium cernuum* with the remark that the history of the subject could be given in a few words, since it was necessary to cite only 3 or 4 investigators. SPRING (2), HOFMEISTER (3), DEBARY (4), FANKHOUSER (5), and BECK (6) are mentioned; but neither SPRING

nor HOFMEISTER ever saw any prothallia. DEBARY, and later BECK, germinated the spores of *L. inundatum*, and FANKHOUSER found a few prothallia of *L. annotinum.*

TREUB overlooked the English surgeon, JOHN LINDSAY (1), who nearly 100 years before had germinated the spores of the very species with which TREUB was dealing. LINDSAY was also the first to raise ferns from the spores. Having noted very young ferns growing in the open in Jamaica, he sowed the spores ("farina") and watched their development. It was in connection with this work that he tried *L. cernuum.* His own account is interesting: "I have very lately sown that fine farina or dust contained in the anthers of a species of the genus *Bryum*, namely, *Bryum caespititium*, or one very like it, and also the farina of *Lycopodium cernuum.* There is a vegetable growth taking place where they were sown which I hope will prove to be their young plants." Later, in a letter to Sir JOSEPH BANKS in regard to *Bryum caespititium* and *Lycopodium cernuum*, he states that he had repeatedy sown them both, and in proper situation found that they grew very readily. There were no further figures or descriptions of either the *Bryum* or *Lycopodium.*

SPRING's failure to germinate spores brought him to the curious conclusion that *Lycopodium*, and also *Psilotum* and *Tmesipteris*, consist exclusively of male plants, the females having been destroyed in some geological catastrophe. At this time it was generally believed that the spores, if they should germinate, would develop directly into the leafy plants. A few years later, HOFMEISTER opposed this view and predicted that the spores would give rise to prothallia bearing antheridia and archegonia, and that the leafy plant would arise from the fertilized egg; but all attempts to prove his theory by germinating the spores resulted in failure.

DEBARY succeeded in germinating the spores of *L. inundatum*, and in 9 days obtained prothallia consisting of 7 cells; but repeated attempts failed to produce more advanced stages, except that one prothallium was observed which had reached the 11-cell stage. The prothallia soon died.

In 1873, FANKHOUSER, in Switzerland, found prothallia and sporelings of *L. annotinum* growing naturally. This fortunate find,

together with the results of DeBary, who had described early stages of *L. inundatum* from cultures, made it possible to make a general outline of the development from the germination of the spore up to the adult prothallium with sporelings attached.

Beck sowed the spores of various species under various conditions, but *L. inundatum* was the only one to germinate and the prothallia did not get beyond the 10-cell stage. He asserted that after 2 years the spores of *L. clavatum* showed chlorophyll and looked as if they were about to germinate, but no cell division occurred.

Since Fankhouser's paper appeared, 3 men have made large contributions to our knowledge of these peculiar prothallia. In 1884, 1886, 1888, and 1889, Treub (**7, 9, 11, 12**) published a splendid series of researches upon the prothallia of Javanese species. In 1885, Bruchmann (**8**) began his patient and persistent researches upon the difficult temperate species with subterranean prothallia which had baffled all previous investigators; and in 1887, Goebel (**10**) found prothallia of *L. inundatum*, so that, with the stages secured by DeBary, he was able to give a connected account of this species.

Treub began his series with an investigation of *L. cernuum*. He germinated the spores of this familiar tropical species and some of the prothallia reached the early antheridium stage before they died. However, he found abundant material growing wild, and so had a complete series from the germination of the spore to the adult prothallium with embryos and older sporelings.

The prothallia are green and grow on the surface of the substratum, the largest reaching a height of 2 mm. When the spore germinates, a more or less spherical body is formed, about 8 or 10 cells in diameter. From the top of this body, which Treub called the "primary tubercle," an alga-like filament then develops, at first consisting of a single row of cells, but soon dividing in all planes, so that a stout cylindrical body is formed more than twice the diameter of the primary tubercle and 5 or 6 times as long. The tip of the cylindrical portion is profusely branched, and at the base of the branches the antheridia and archegonia are borne. The embryogeny is particularly interesting, since the fertilized egg does

not develop directly into a leafy plant, but produces a protocorm with protophylls, resembling a miniature *Phylloglossum.*

TREUB (9) next dealt with *L. Phlegmaria*, another familiar tropical species, epiphytic upon trees. The prothallia are found on the tree trunks just below the surface of the humus, but they have no chlorophyll, being entirely saprophytic and abundantly supplied with an endophytic fungus. The main body is tuberous, about 2 mm. in diameter, more or less spherical or somewhat elongated, and has several branches extending in various directions. The branches vary from 1 to 6 mm. in length and bear antheridia or archegonia or reproductive bodies which TREUB called "propagula." The antheridia and archegonia are usually at the tips of the branches, not at the base as in *L. cernuum*. The propagula are of two general types, one consisting of scores or even hundreds of cells forming a flask-shaped body with a slender stalk of one or two cells; the other is much smaller, more or less spherical in shape, and consists of only a few cells, usually not more than 2 or 3, with the outer walls very much thickened. In the first type the propagula break off at the stalk and grow directly into new prothallia, while in the second type there is a more or less prolonged resting period. The first type seems to correspond to the gemmae of liverworts and mosses, and the second type seems to correspond to the brown bulbils of mosses.

TREUB was not able to germinate the spores, and he believed that most of the prothallia found in nature come from propagula, prothallia from spores being comparatively rare.

The accounts of the development of antheridia, archegonia, and embryo are very complete, but the vascular anatomy of the sporeling is not described.

The prothallia of *L. salakense* are aerial, green, have no endophytic fungus, and are the only ones which TREUB succeeded in raising from the spore to the adult stage with antheridia and archegonia. In a few days the prothallia developed to the primary tubercle stage, then rested for several months, and finally resumed their growth and completed the life history. As in *L. cernuum*, a simple filament appears at the top of the primary tubercle and then forms a cylindrical body several cells in thickness, but other fila-

ments then develop and behave in the same manner, so that there are several branches. The antheridia and archegonia are formed at the tops of these branches, there being no leaflike organs as in *L. cernuum* and *L. inundatum.*

The prothallia of *L. carinatum*, *L. Hippuris*, and *L. nummulariforme* are all of the *L. Phlegmaria* type, those of *L. carinatum* bearing such a close resemblance that TREUB (11) warns prospective collectors against collecting in localities where both species occur, since it is impossible to distinguish either the prothallia or the embryos. The prothallia of *L. Hippuris* are similar, but are more vigorous and the branches are thicker. TREUB was not able to disentangle complete prothallia of *L. nummulariforme* from the substratum and so had to write his account from fragments. He did not find any endophytic fungus.

The final paper in TREUB'S (12) series dealt with the embryo of *L. cernuum.* The series of stages was very complete, from embryos consisting of a few cells, through the protocorm stages, and up to sporelings with a few leaves. After the embryo has developed a protocorm with protophylls resembling a small *Phylloglossum*, a definite growing point is organized which develops into a leafy axis and at the same time the first root appears. TREUB indicated the course of the vascular bundles, but did not make any further study of the anatomy. He regarded the protocorm as a recapitulation of a *Phylloglossum* stage in the ancestry of *Lycopodium.*

In 1884, the same year that TREUB (7) began his research upon tropical forms, BRUCHMANN (8) found 3 prothallia of *L. annotinum*, and thus began a series of researches which extended over 25 years and resulted in clearing up the life-histories of the much more difficult temperate species. BRUCHMANN'S first paper appeared in 1885, but TREUB'S first account, although dated 1884, appeared at about the same time, so that neither knew the other was working upon prothallia. BRUCHMANN'S (13) most extensive work, which gained him the prize of the Paris Academy of Science, appeared in 1898, and contained descriptions of *L. clavatum*, *L. annotinum*, *L. complanatum*, and *L. Selago.* All were found growing in the Thuringer forest near Gotha, but the germination of the spores and earliest stages in the development were lacking. The development

of antheridia, archegonia, and embryos are very clearly described. Ten years later this account was supplemented by a very complete description of *L. complanatum*. Although BRUCHMANN (15) had made repeated efforts to germinate the spores of various species, he met only the failures which had discouraged other botanists; but finally his perseverance was rewarded and he was able to give a complete account of the germination and early development of *L. clavatum*, *L. annotinum*, and *L. Selago*. The surprising feature is the long-delayed germination. The spores of *L. Selago* germinated in 3–5 years, and the development of antheridia and archegonia was complete in 6–8 years; *L. clavatum* and *L. annotinum* were even slower, germinating in 6–7 years and requiring 12–15 years to complete the development of antheridia and archegonia. BRUCHMANN suggests that possibly the periods might be shortened artificially if the proper stimuli could be discovered. All the species reported in BRUCHMANN'S various papers are subterranean and saprophytic, but the spores germinate independently and develop to the 4 or 5-cell stage, and at this stage the fungus must enter or there will be no further development.

L. salakense, which TREUB (11) succeeded in keeping in cultures throughout the whole life history, is green, aerial, has no fungus, and germination takes place in a few days. *L. cernuum* is also aerial and green and germinates with equal promptness, but it does not develop beyond the primary tubercle stages unless the fungus enters. *L. inundatum* in DEBARY'S cultures developed to an early primary tubercle stage with some chlorophyll and then died. The subsequent work of GOEBEL (10), who found prothallia growing naturally, proved that this species also has an aerial, green prothallium with an endophytic fungus. In *L. cernuum* and *L. inundatum*, however, the fungus infection is much slighter than in the saprophytic species.

So far as I have been able to determine, there is only one paper which makes any mention of the prothallia of New Zealand species of *Lycopodium*, and this paper by HOLLOWAY (16) deals primarily with the anatomy of the sporophyte. The investigation, both in the field and in the laboratory, is of such high grade that we hope HOLLOWAY will sometime give us an extended account of the pro-

thallium and the anatomy of the sporeling. The varied species, ranging from epiphytes to ground forms, with prothallia ranging from the green, leafy aerial type to the deepest subterranean tuberous type, make New Zealand an ideal place for such a study.

Material and observations

The epiphytic type is not represented in the species at my disposal. *Lycopodium laterale* has a stout creeping rhizome, with numerous erect branches, and cones borne laterally; *L. scariosum* has a somewhat similar habit, except that the cones are terminal; *L. volubile* is the most beautiful species of the genus, bearing a striking resemblance to *Selaginella* as it trails along the ground or over bushes; but, unlike *Selaginella*, it keeps well after being gathered and is much used for table decoration.

PROTHALLIA

L. LATERALE.—The only reference I have been able to find in regard to the prothallium of this species is in HOLLOWAY'S (**16**) paper. He says "in the case of *L. laterale* prothallial plants were found in two localities, growing on recently overturned marshy soil. The prothallus of this species corresponds to the type of *L. cernuum*, is small and short-lived, and is situated at the surface of the ground."

I had at my disposal 3 prothallia with protocorms attached and one older protocorm entirely free from the prothallium. In the first 3, each of the protocorms bore 2 fully grown protophylls; the older protocorm bore 10 protophylls. Two of the prothallia with their young plants are shown in figs. 1 and 2, the exact size being indicated in fig. 1*a*. The older protocorm with its 10 protophylls is shown in fig. 3. In fig. 1 the particles of sand and soil are not represented.

The upper half of the prothallium projects above the surface of the soil. There is a more or less spreading crown of leafy lobes, abundantly supplied with chlorophyll, and at the base of the inner face of these lobes the antheridia and archegonia are borne. It seems evident that the base of the prothallium was first to develop, but no sharply differentiated primary tubercle, like that shown in

TREUB'S figures of *L. cernuum*, was found in these specimens. However, the base of the prothallium is more pointed than in *L. cernuum*, and this pointed base may represent the primary tubercle.

In proportion to the size of the prothallium, the protocorm is much more massive than in *L. cernuum*. There is no single, definitely organized growing point giving rise to all the protophylls, but rather a series of points, each giving rise to a protophyll. Stomata are abundant almost to the base of the protophyll; they are of the simplest type and open into a loose parenchyma with large air spaces. The transverse section is circular and shows a single weak vascular strand extending a short distance into the protocorm and ending blindly, without uniting with the strands of neighboring protophylls. The protuberance shown in front of the large protophyll in fig. 2 might be mistaken for the growing point from which the leafy axis is to be developed, but that point is formed much later, after several protophylls have appeared. The prothallium and protocorm shown in fig. 2 are similar, but indicate that there is considerable variation in both structures. Outlined against the protocorm is a second embryo.

The much older protocorm (fig. 3) indicates that the protophylls arise at irregular points, although there is a general progression, so that the protocorm resembles a very short horizontal rhizome. The 2 protophylls in the foreground are evidently the first ones formed, and the 3 much smaller ones at the left are the latest. The leafy axis of the permanent plant has not yet appeared. This specimen and also those shown in figs. 1 and 2 were sectioned, but the soil prevented satisfactory results. However, the sections showed the position of sex organs, the distribution of the fungus, and the relation of the protocorm to the prothallium. These features are shown, in a very diagrammatic way, in fig. 1*b*.

L. laterale belongs definitely to the type represented by *L. cernuum* and *L. inundatum*, since it has a short-lived green prothallium and an ephemeral protocorm with protophylls preceding the permanent leafy plant. *L. salakense* also belongs here, since the prothallium is green, and in its earlier stages behaves like that of *L. cernuum;* but it differs from the other 3 in having no endophytic

fungus. Whether it has a protocorm stage is not known. TREUB failed to find sporelings when he made his first investigation; later, in his work on the embryogeny of *L. cernuum*, he figures a protocorm stage in *L. salakense*.

It is interesting to note that the protocorm stage has been found only in *L. cernuum*, *L. salakense*, *L. inundatum*, and *L. laterale*, all of which have spores which germinate, giving rise to green short-lived prothallia. The spore-bearing plants of all 3 species, as well as that of *L. salakense*, grow upon the ground. No green prothallium or a protocorm phase in the embryogeny has yet been reported for any epiphytic *Lycopodium*.

L. VOLUBILE.—The only reference to the prothallium of this species is by HOLLOWAY (**16**). He says "the prothallus is large, firm, and long-lived. Healthy prothalli were seen still attached to sporelings which were as much as 10 cm. in length. Generally the prothalli are subterranean, being buried 1–4 cm. in depth; in several instances, however, they were observed growing on the surface of the ground, and the upper portion of the prothallus was then well supplied with chlorophyll."

The material at my disposal included 9 prothallia and 2 sporelings, one of them still attached to the prothallium (figs. 4–9). All belong to the subterranean tuberous type, and 4 of them (figs. 4, 5, 8, and 9) show a primary tubercle. Although the material is somewhat limited, it is evident that there is considerable variation in size and form.

The endophytic fungus is most abundant midway between the center and the surface, and is entirely lacking in the crown, in the upper part of the depression within the crown, and in the axis of the prothallium. Cells with considerable fungus abut directly upon those with none at all, making a sharp contrast (fig 12). A detail is shown in fig. 13.

The crown is differentiated into two regions in some places, only the inner one of which bears archegonia and antheridia, as shown in figs. 5 and 6; but even in these 2 prothallia some portions of the crown show no such differentiation, and the prothallia shown in figs. 7 and 8 have uniformly rounded crowns with no indication of two regions. While most of the sex organs are on the swollen rim

of the crown, they are not confined to this region, but occur in scattered patches within the rim on any part of the depressed region. A sectional view of a typical distribution of archegonia, antheridia, and the fungus region is shown in fig. 14.

The antheridia vary in size, shape, and output of sperms. They form hemispherical projections, with a nearly spherical mass of sperms; or they project scarcely at all, in which case the mass of sperms is not quite so regular. In a few cases, the sperm mass was elongated, making the topography bear some resemblance to that of an archegonium. In all cases, only one layer of cells separates the sperms from the surface, so that the essential course of development is uniform. A typical view is shown in fig. 15.

The foot of the sporophyte is strongly haustorial, and the cells surrounding it have some starch but very little protoplasm or other visible contents; consequently, the food supply must come largely from the fungus region and must be in a liquid condition even at a considerable distance from the foot. This is quite different from the condition in some gymnosperms, where only a single layer of cells may separate the haustorial cells of the embryo from those containing an abundance of food material in solid form. The foot is small and the vascular strand does not extend into it, but extends in an unbroken line from the shoot into the root, which is very late in developing. However, a few elongated cells, which do not become lignified, bend away from the main axis and point toward the foot.

L. SCARIOSUM.—The only description of this species is that given by HOLLOWAY (**16**), who says "the prothallus of *L. scariosum* was discovered in two localities. Like that of *L. volubile*, it appears to correspond to the *L. clavatum* type. It is large, firm, and long-lived, and in every case was found deeply buried (2–6 cm.)." Three specimens of this species were available and all had reached maturity, one bearing a young plant 18 mm. long, and the other two showing the foot and base of younger sporophytes which had broken off. Both prothallium and sporeling are larger and coarser than in *L. volubile*, as can be seen by comparing figs. 9 and 11, which are drawn to the same scale. The prothallium is densely infested by the fungus, which has about the same distribution as in *L. volubile*.

ORIGIN OF THE SUBTERRANEAN HABIT.—That the green leafy prothallia represent the original type from which the subterranean forms have diverged can scarcely be doubted. The species with green, leafy prothallia (*L. cernuum*, *L. inundatum*, *L. salakense*, and *L. laterale*) have spores which, in the first 3 species, are known to germinate immediately; while in all those with subterranean prothallia the spores germinate only after a long resting period. It would seem that some change has occurred in the spore which has delayed the germination; and then only such spores as reached a protected situation would survive to germinate at all. Germinating in protected situations, with little or no light, the prothallia naturally would assume the forms of subterranean, dependent structures. That this has been the order of regression is indicated by the fact that the leafy crown has not been lost altogether, but only modified. In *L. annotinum*, as described by BRUCHMANN, the prothallium is subterranean and saprophytic, but still retains some of the leafy appearance; in *L. laterale* the crown is sometimes broken up into separate fleshy cushions which may represent leafy lobes; in more extreme cases, there is merely a swollen, fleshy rim to represent the leafy structure. The position of antheridia and archegonia is about the same as in the green, leafy forms.

If those who are expert in hastening the germination of seeds which normally have a long resting period, could find some way to make the spores of *L. annotinum*, or some such species, germinate immediately, it would not be surprising if green, leafy prothallia should appear.

ANATOMY OF THE SPOROPHYTE

In the vascular structure of the adult sporophyte *Lycopodium* still presents some difficult problems, although investigations like those of HILL and others have cleared up some of the phases. However, it seems likely that the final solution will come through a comparative study of sporelings, intermediate stages, and adult plants. TREUB (7), BRUCHMANN (13), Miss WIGGLESWORTH (14), and HOLLOWAY (16) have figured and described a few sections; but material has been scanty or other features of the problem have so engrossed the attention that this important feature has received little attention.

It would be dangerous to draw any serious conclusions from a study of 2 or 3 sporelings, all of which had reached the leafy stage; but, in the present condition of the subject, it seems worth while to describe a few features. The study was made from the sporelings shown in figs. 9–11.

In *L. volubile* the foot is quite small, and although somewhat larger in *L. scariosum*, no vascular strand extends into it, but a few cells, not lignified, point in its direction. The vascular strand extends in an unbroken line from the tip of the stem to the tip of the root, which in both species is late in appearing.

The sporeling of *L. volubile* shown in fig. 9, and that of *L. scariosum* shown in fig. 10, were sectioned transversely down to the crown of the prothallium, and the portion below the crown was then cut longitudinally. It would have been much better if transverse sections had been continued throughout. In both species the leaves are surprisingly like the protophylls of *L. laterale*. Throughout a considerable portion of their length the transverse section is circular, and even in the broader middle region the leaves are thick and spongy, consisting almost entirely of very loose parenchyma with large intercellular spaces and a single vascular strand. Stomata are irregularly scattered over the entire surface (fig. 16). The adult leaves in both species are rather thin.

In *L. scariosum* the shifting topography of the stele is a conspicuous feature, especially in the upper, leafy region; in the lower half of the sporeling, where there are only a few scale leaves with no leaf traces, the arrangement is more uniform. Near the middle of the leafy portion, a hexarch, pentarch, and tetrarch condition occurs within a vertical distance of 1 mm. Throughout the lower one-third of this specimen the stele is rather constantly tetrarch; but, just above the foot a few sections show a triarch and even a diarch stele. That the leaf traces connect with the protoxylem points is evident at a glance; but whether the leaf traces determine the topography is not so clear. However, it is significant that the stele is more complex in the leafy region and that it attains its greatest complexity in mature plants with larger leaves and vigorous leaf traces. In various places there are indications of the banded arrangement characteristic of the adult stele.

The differentiation of the vascular tissues is interesting. A short distance below the meristem the large cells which are to form the largest tracheids are easily recognized, and some of the cells of the points of the radial structure can be distinguished, although lignification has not yet begun. Very soon the points of the radial structure begin to lignify and are then marked off very sharply from the surrounding tissues (fig. 17). These patches of lignified tissue consist almost exclusively of coarsely pitted tracheids. It is possible that there are some spiral vessels, but it looks as if practically all of the spirally marked cells belong to the leaf traces. If protoxylem is to be identified by spiral and annular markings, very little of the tissue which becomes lignified at this early stage would satisfy such a criterion; but the tissue is so well defined and becomes lignified so far in advance of the rest of the xylem, and is so sharply marked off from the large cells which in longitudinal view have the typical scalariform marking, that it may very properly be called the protoxylem. It should be recalled that in the cycads spiral vessels in the protoxylem are largely confined to the seedling, the protoxylem of the adult plant consisting almost exclusively of tracheids.

The study of the root was not satisfactory. Near the tip the bundle is C-shaped and diarch with the phloem in the sinus.

The sporeling of *L. volubile* is comparatively slender and in every way more delicate than that of *L. scariosum*. In the upper leafy portion the stele is quite regularly radial and tetrarch; but from the secondary root (*r* in fig. 9) down to the prothallium the structure is regularly or irregularly triarch. In connection with the more uniform topography of this stele, it should be noted that the leaves and their single vascular strand are not nearly so robust as in *L. scariosum*. The adult stele has the banded arrangement. The differentiation of the tissues of the stele proceeds as described for *L. scariosum*.

Summary

1. *Lycopodium laterale* has a green, leafy prothallium, and there is a protocorm-protophyll stage in the embryogeny. *L. volubile* and *L. scariosum* have subterranean prothallia with no protocorm stage, but the early leaves have the structure of protophylls.

2. In *L. scariosum* and *L. volubile* the sporeling has a radial stele. The adult plants have a banded stele.

3. The outer part of the ray of the radial structure consists almost exclusively of pitted tracheids with scarcely any spiral vessels, but becomes lignified long in advance of the large tracheids of the metaxylem, and should be regarded as the protoxylem.

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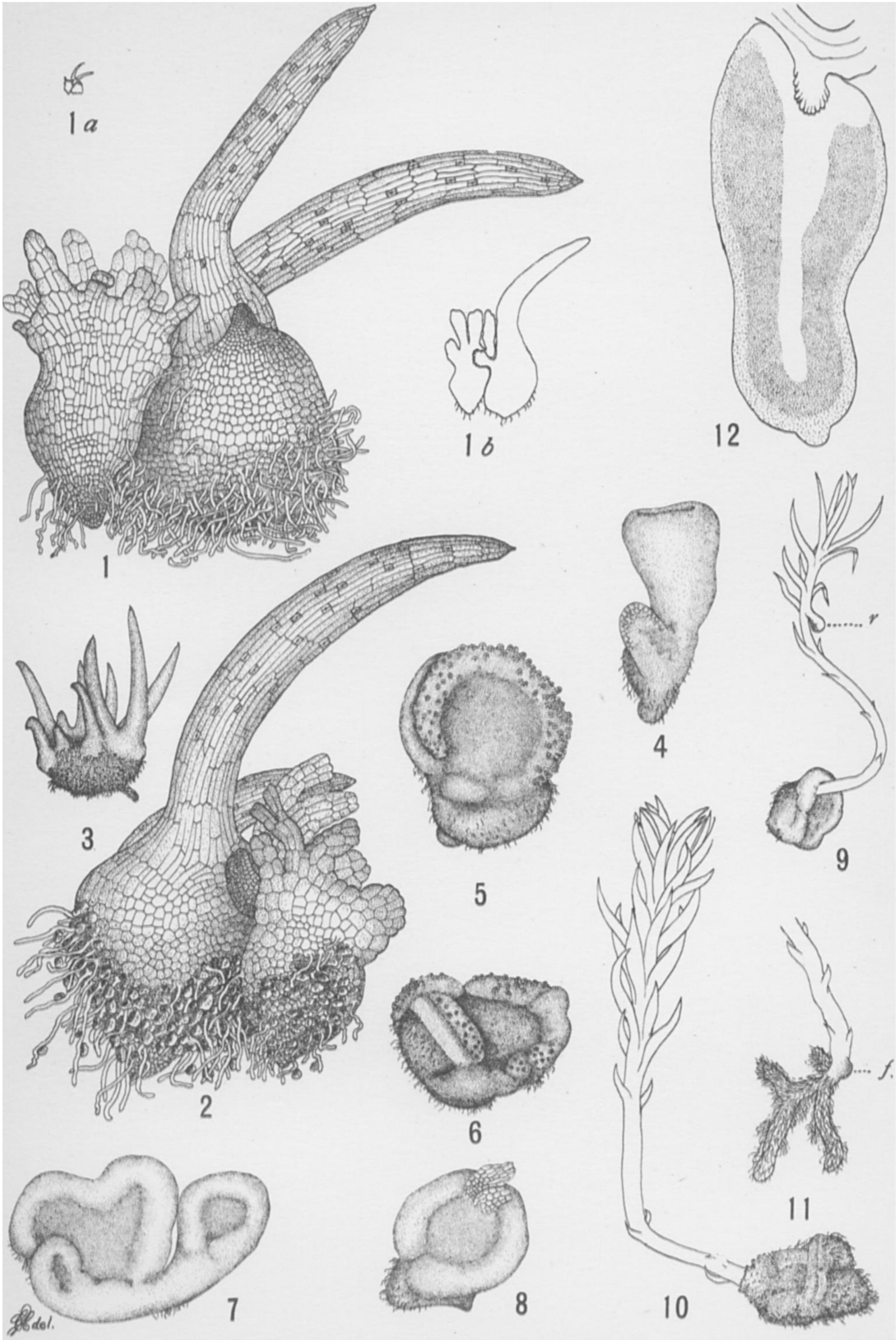
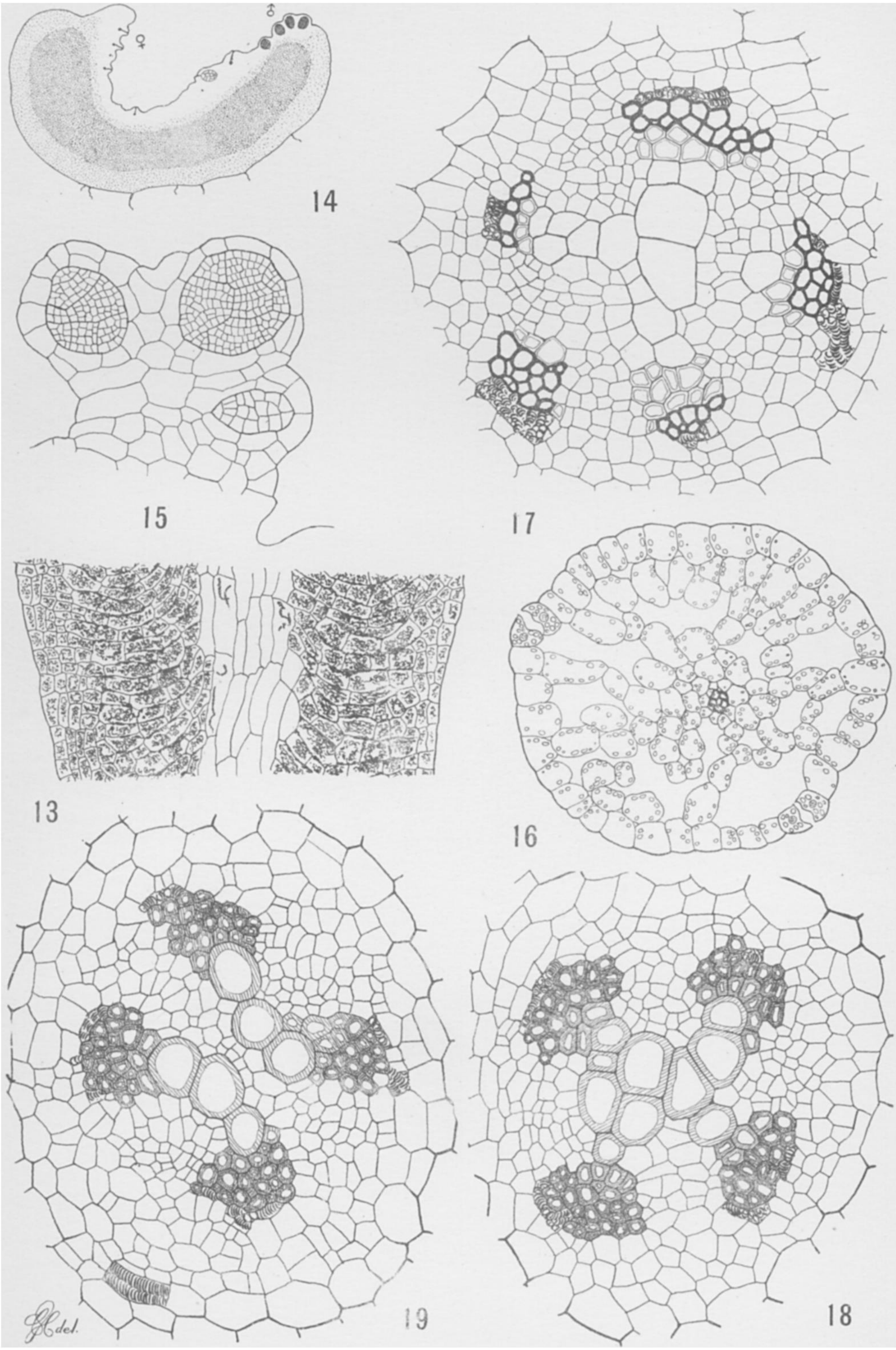
LITERATURE CITED

1. LINDSAY, JOHN, Account of the germination and raising of ferns from the seed. Trans. Linn. Soc. **2**:93–100. *pl. 18.* 1794.
2. SPRING, A. F., Monographie de la famille des Lycopodiacées. 1842.
3. HOFMEISTER, W., Vergleichende Untersuchungen höherer Kryptogamen. 1851.
4. DEBARY, A., Sur la germination des Lycopodées. Ann. Sci. Nat. Bot. IV. **9**:30–36. *pl. 4.* 1858 (published almost simultaneously in other places).
5. FANKHOUSER, L., Über den Vorkeim von *Lycopodium.* Bot. Zeit. **31**:1–6. *pl. 1.* 1873.
6. BECK, G., Einige Bemerkungen über den Vorkeim von *Lycopodium.* Oesterreich. Bot. Zeit. **30**:341–344. 1880.
7. TREUB, M., Études sur les Lycopodiacées. I. Le prothalle du *Lycopodium cernuum* L. Ann. Jard. Buitenzorg **4**:107–138. *pls. 9–17.* 1884.
8. BRUCHMANN, H., Das Prothallium von *Lycopodium.* Bot. Centralbl. **21**:23–28, 309–313. *pl. 1.* 1885.
9. TREUB, M., Études sur les Lycopodiacées. II. Le prothalle du *Lycopodium Phlegmaria* L. Ann. Jard. Buitenzorg **5**:87–114. *pls. 11–22.* 1886; III. Le développement de l'embryo chez *L. Phlegmaria.* **5**:115–139. *pls. 23–31.* 1886.
10. GOEBEL, K., Über Prothallien und Keimpflanzen von *Lycopodium inundatum.* Bot. Zeit. **45**:161–168. *pl. 2.* 1887.
11. TREUB, M., Études sur les Lycopodiacées. IV. Le prothalle du *Lycopodium salakense.* Ann. Jard. Buitenzorg **7**:141–146. *pls. 16–18.* 1888; V. Les prothalles des *Lycopodium carinatum, nummulariforme,* et *Hippuris. ibid.,* 146–150. *pl. 19.*
12. ———, Études sur les Lycopodiacées. VI. L'embryon et la plantule du *Lycopodium cernuum* L. Ann. Jard. Buitenzorg **8**:1–14. *pls. 1–5.* 1890; VII. Les tubercles radicaux du *Lycopodium cernuum* L. *ibid.* 15–22. *pls. 6–12;* VIII. Considerations théoretiques. *ibid.* 23–37.
13. BRUCHMANN, H., Über die Prothallien und die Keimpflanzen mehrerer Europäischer Lycopodien. pp. 119. *pls. 1–8.* 1898.



CHAMBERLAIN on LYCOPODIUM



CHAMBERLAIN on LYCOPODIUM

14. WIGGLESWORTH, GRACE, The young sporophytes of *Lycopodium complanatum* and *L. clavatum*. Ann. Botany **21**:211–234. *pl. 22*. 1907.

15. BRUCHMANN, H., Die Keimung der Sporen und die Entwickelung der Prothallien von *Lycopodium clavatum*, *L. annotinum*, und *L. Selago*. Flora **101**:220–267. *figs. 35*. 1910.

16. HOLLOWAY, J. E., A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. New Zealand Inst. **42**:356–370. *pls. 31–34*. 1910.

EXPLANATION OF PLATES II–III

FIG. 1.—*Lycopodium laterale:* prothallium with leafy crown at left and bearing, at right, a protocorm with 2 fully grown protophylls and one young protophyll; ×20 (fig. 1*a* shows this plant natural size; fig. 1*b* is sectional view).

FIG. 2.—*L. laterale:* prothallium, at right, bearing a protocorm with 2 protophylls and also a second embryo; the soil and sand have not been removed; ×20.

FIG. 3.—*L. laterale:* protocorm with 10 protophylls; ×6.

FIG. 4.—*L. volubile:* prothallium showing primary tubercle at base; the crown is very even; ×10.

FIG. 5.—*L. volubile:* prothallium showing crown with numerous archegonia and antheridia; primary tubercle at base; ×10.

FIG. 6.—*L. volubile:* prothallium with archegonia and antheridia; the crown is lobed; ×10.

FIG. 7.—*L. volubile:* large, irregular prothallium; ×10.

FIG. 8.—*L. volubile:* prothallium with 2 young sporophytes; ×10.

FIG. 9.—*L. volubile:* prothallium with sporeling; a secondary root is shown at *r;* ×4.

FIG. 10.—*L. scariosum:* prothallium with sporeling; ×4.

FIG. 11.—*L. scariosum:* lower part of a young sporeling showing roots and foot; ×4.

FIG. 12.—*L. volubile:* diagrammatic view of prothallium with foot and lower part of sporeling.

FIG. 13.—*L. volubile:* detail of prothallium.

FIG. 14.—*L. volubile:* diagrammatic sectional view of prothallium showing archegonia, antheridia, and distribution of fungus, the latter indicated by shading.

FIG. 15.—*L. volubile:* portion of prothallium showing antheridia.

FIG. 16.—*L. volubile:* transverse section of leaf.

FIG. 17.—*L. scariosum:* transverse section of stem of sporeling before the large tracheids become lignified; *px*, protoxylem; *p*, phloem.

FIG. 18.—*L. scariosum:* same sporeling lower down; large tracheids have become lignified.

FIG. 19.—*L. scariosum:* same sporeling showing indication of banded arrangement.